

Phenotypic plasticity of *Artemisia ordosica* seedlings in response to different levels of calcium carbonate in soil

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Abstract: Plant phenotypic plasticity is a common feature that is crucial for explaining interspecific competition, dynamics and biological evolution of plant communities. In this study, we tested the effects of soil CaCO_3 (calcium carbonate) on the phenotypic plasticity of a psammophyte, *Artemisia ordosica*, an important plant species on sandy lands in arid and semi-arid areas of China, by performing pot experiments under different CaCO_3 contents with a two-factor randomized block design and two orthogonal designs. We analyzed the growth responses (including plant height, root length, shoot-leaf biomass and root biomass) of *A. ordosica* seedlings to different soil CaCO_3 contents. The results revealed that, with a greater soil CaCO_3 content, *A. ordosica* seedlings gradually grew more slowly, with their relative growth rates of plant height, root length, shoot-leaf biomass and root biomass all decreasing significantly. Root N/P ratios showed significant negative correlations with the relative growth rates of plant height, shoot-leaf biomass and root length of *A. ordosica* seedlings; however, the relative growth rate of root length increased significantly with the root P concentration increased, showing a positive correlation. These results demonstrate that soil CaCO_3 reduces the local P availability in soil, which produces a non-adaptive phenotypic plasticity to *A. ordosica* seedlings. This study should prove useful for planning and promoting the restoration of damaged/degraded vegetation in arid and semi-arid areas of China.

Keywords: *Artemisia ordosica*; N/P ratio; phenotypic plasticity; relative growth rate; soil CaCO_3 ; soil P availability; arid and semi-arid areas

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1 Introduction

Phenotypic plasticity is the phenotypic characterization produced by the same genotype in response to different local environmental conditions (Bradshaw, 1965; Lauri et al., 2016; Li et al., 2016). It is inherently a developmental and multivariate phenomenon (Pigliucci et al., 1997). A variety of environmental factors, such as light, temperature, water, heat and wind, jointly or in isolation, can induce phenotypic plasticity (Sultan, 2001a, b; Pigliucci and Kolodnynska, 2002). Importantly, the plasticity of specific functional traits itself may be inheritable and thus be capable of independently evolving under natural selection (Jain and Bradshaw, 1966; Stearns, 1989; D'Ambrosio and Colagè, 2017). Quantifying the phenotypic plasticity of plants can reveal the relationship between an individual's phenotypic plasticity and its ecological and evolutionary patterns (Schlichting, 1986; Bradshaw and Hardwick, 1989; Pigliucci, 2005). Moreover, being

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sessile organisms, phenotypic plasticity helps plants to cope with sudden environmental changes (Via et al., 1995; Pigliucci, 2002; Bossdorf and Pigliucci, 2009) and can facilitate species invasions (Geng et al., 2004) and affect patterns of evolutionary diversity (Ghalambor et al., 2007; Fusco and Minelli, 2010; Storz et al., 2010).

At 10°–40° latitudes in both hemispheres, soil generally contains CaCO_3 (calcium carbonate) (Schinas and Rowell, 1977). Abbas et al. (1991) classified plant species as either calcicole (a plant species that thrives in lime-rich soil), calcifuge (a plant species that does not grow well in lime-rich soil), or CaCO_3 -indifferent species based on their ability to survive on CaCO_3 -rich soil. Almost 57 years ago, Lee and Woolhouse (1971) investigated the effects of bicarbonate on the root growth of a number of calcicole and calcifuge grasses, and found that root growth of calcifuge species was more strongly inhibited by soil CaCO_3 than that of calcicole species. Interestingly, in a pot experiment, Pedersen et al. (2011) indicated that both a calcicole species, *Anisantha tectorum*, and a calcifuge species, *Rumex acetosella*, grew slower in subsoil containing approximately 10% CaCO_3 than in topsoil with less than 1% CaCO_3 . Results from our previous study suggested that the ratio of soil CaCO_3 to available P could significantly influence the plant density of *Artemisia ordosica* populations (Zhao et al., 2012), indicating that soil CaCO_3 might induce phenotypic plasticity in this plant species.

It is intriguing to ask, since CaCO_3 itself is a kind of substrate that forms soil, how might soil CaCO_3 induce plant phenotypic plasticity? We hypothesized that soil CaCO_3 limits P availability in soil, preventing P absorption by plant, thereby affecting the N/P ratio, growth rate, and phenotypic plasticity of plant. In this study, we chose *A. ordosica* for use in three pot experiments, in which its phenotypic plasticity was analyzed under varying soil CaCO_3 contents. The aims of this study were: (1) to examine the effect of soil CaCO_3 content on the phenotypic plasticity of *A. ordosica*, and (2) to explore the possible mechanisms underlying the relationship between soil CaCO_3 content and plant phenotypic plasticity in arid and semi-arid environments.

2 Materials and methods

2.1 Greenhouse pot experiments

Artemisia ordosica, is a dominant species of psammophyte communities that form on sandy lands in arid and semi-arid areas of Northwest China. The restoration of plant communities dominated by *A. ordosica* is currently of great importance for controlling degraded vegetation ecosystems in the region of study (Wang et al., 2018).

The pot experiments described below were conducted at the greenhouse of the Department of Plant Biology and Ecology, Nankai University, China, in March 2012. The seeds of *A. ordosica* and the soil used in the pot experiments were collected from Bayanhot of Alagxa Left Banner, Inner Mongolia Autonomous Region, China.

To investigate the ability of *A. ordosica* to grow in soil differing in its CaCO_3 contents, we performed three pot experiments with a two-factor randomized block design and two orthogonal designs. In the low soil CaCO_3 content orthogonal experiment with an L_8 (4×2^4) array, the levels of soil CaCO_3 content were 0 (control), 10, 25 and 50 g/kg. In the high soil CaCO_3 content orthogonal experiment with L_{16} (4^5) array, the levels of soil CaCO_3 content were 0 (control), 25, 50 and 100 g/kg, the levels of soil available P were 0, 3, 6 and 12 g/kg, and the levels of watering amount were 200, 250, 300 and 350 mL/week. In the two-factor randomized block experiment with high soil CaCO_3 content, the soil CaCO_3 levels were 10, 50, 75 and 100 g/kg, and the watering levels were 250, 300, 350 and 400 mL/week, respectively. In all three pot experiments, each treatment was applied three times.

The seed sowing process went as follows. Seeds were sown with 3 or 4 seeds per hole on a seedling-raising pan filled with a 1:1 mixture of turf:perlite. The pan was then covered with a thin moist paper-film to reduce evaporation until the seeds had germinated. After 25 d, we transferred the germinated seedlings to polyvinyl chloride (PVC) pots (170 mm \times 200 mm; 1 seedling per pot) according to the experimental design. Each pot was filled with 2 kg of mixed soil at a ratio of 2:1

of sandy soil:loam. This soil mixture contained 3.11 g/kg organic matter, 7.00 mg/kg available N, and 5.77 mg/kg available P.

To calculate the relative growth rate (RGR) of potted seedlings, we measured and recorded all their starting plant heights upon transferring them to the PVC pots. From the seedling-raising pan, leftover *A. ordosica* seedlings ($n=50$) served as initial control seedlings were dug out and washed with water to remove mud on their roots, with any bulk water soaked up by filter papers. Then, we measured and recorded the plant height, root length, and fresh weights of shoot-leaf biomass and root biomass.

Then the *A. ordosica* seedlings grow for a 40-d monitoring period. To avoid excess water evaporation, we watered all the seedlings by using a syringe to inject the water beneath the soil surface to a depth of 2 cm. The greenhouse growing temperature was kept at 25°C during the daytime and at 18°C during the nighttime.

Once harvested whole from the pots, we measured and recorded the plant height, root length, shoot-leaf biomass and root biomass of every seedling.

2.2 Sample analyses

For the *A. ordosica* seedlings in the high soil CaCO_3 content experiment, plant N and plant P were determined by the $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$ -semi-micro-Kjeldahl and $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2\text{-Mo-Sb-Vc}$ -colorimetry methods, respectively (Bao, 2007). Three measurement replicates were performed for each plant sample (root).

2.3 Calculation of RGR

A total of 50 leftover *A. ordosica* seedlings were used in curve regressions, with plant height as the independent variable and shoot-leaf biomass, root length and root biomass separately as dependent variables. Because these regression equations were all significant ($P<0.001$), they were used for deriving estimates of the pre-experiment shoot-leaf biomass, root length and root biomass of the potted seedlings.

The RGR values of plant height, root length, shoot-leaf biomass and root biomass of *A. ordosica* seedlings were calculated as follows:

$$\mu = \ln([M_t/M_0])/t, \quad (1)$$

where μ is the relative growth rate of plant height (cm/cm/d), root length (cm/cm/d), shoot-leaf biomass (g/g/d) or root biomass (g/g/d); M_0 is the observed plant height (cm) from pre-experiment or shoot biomass (g), root length (cm), or root biomass (g) predicted from the regression equations; M_t is the post-experiment measurements of the four growth response variables; and t is the growing time (40 d).

2.4 Data analysis

The data were analyzed using SPSS 13.0 software (SPSS, Chicago, Illinois, USA) to perform two-way ANOVA. Homogeneity tests were applied first and Duncan test were then used to test the statistical significance of the means between groups if their variances were equal. Alternatively, Tamhane's T_2 was used to compare means between groups if their variances were different.

3 Results

3.1 Effects of low soil CaCO_3 content on *A. ordosica* seedling growth

In the low soil CaCO_3 content orthogonal experiment, the plant height, root length, shoot-leaf biomass and root biomass of *A. ordosica* seedlings treated with 50 g/kg of soil CaCO_3 was 69.29%, 46.18%, 87.88% and 66.75% lower than those in the control, respectively. As shown in Figure 1, the RGR values of all four growth response variables were lowest under the highest level of soil CaCO_3 content and highest under the lowest level of soil CaCO_3 content.

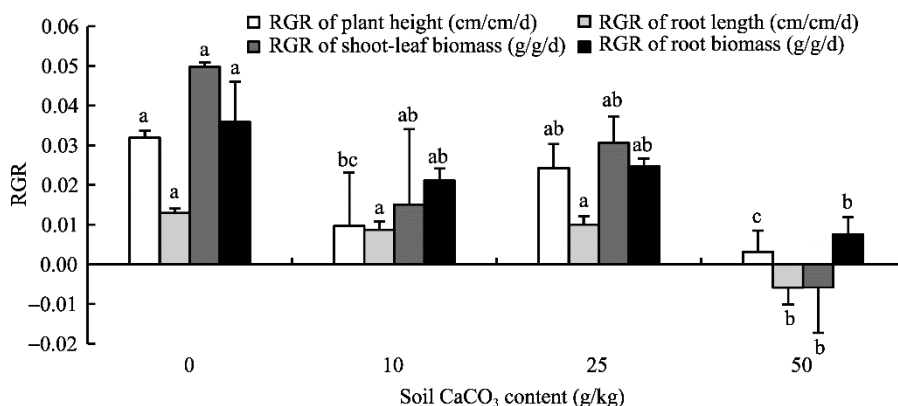


Fig. 1 Growth responses of *Artemisia ordosica* seedlings in the low soil CaCO₃ content orthogonal experiment. RGR, relative growth rate. Different lowercase letters indicate significant differences among soil CaCO₃ contents at $P < 0.05$ level. Bars mean standard errors.

3.2 Effects of high soil CaCO₃ content on *A. ordosica* seedling growth

In the high soil CaCO₃ content experiment with two-factor randomized block design, as the soil CaCO₃ content increased, the RGR values of plant height and shoot-leaf biomass of *A. ordosica* seedlings decreased significantly, while the RGR values of root length and root biomass were also generally reduced but not significantly (Fig. 2a). In this two-factor randomized block experiment, the treatment effect on every growth response variable was not significant ($P > 0.05$) among the four watering levels applied (data not shown).

In the high soil CaCO₃ content experiment with orthogonal design, the treatment effects of soil available P and watering amount on every growth response variable were all not significant ($P > 0.05$) among the treatments (data not shown). Soil CaCO₃ content did not significantly influence the RGR values of plant height, shoot-leaf biomass and root biomass, but it did significantly negatively impact the RGR of root length (Fig. 2b).

3.3 Relationships of RGR of growth response variable with root N/P ratio and root P concentration of *A. ordosica* seedlings

The regression analyses showed that, under the high soil CaCO₃ content, *A. ordosica* seedlings with higher root N/P ratios had low RGR values of plant height (Fig. 3a) and shoot-leaf biomass (Fig. 3b) in the two-factor randomized block experiment and low RGR of root length in the orthogonal experiment (Fig. 3c). A significant positive logarithmical relationship was observed between RGR of root length and root P concentration in the orthogonal experiment (Fig. 3d). That is to say, the RGR of root length in *A. ordosica* seedlings decreased significantly as the root N/P ratio increased while increased significantly as the root P concentration rose.

4 Discussion

Soil CaCO₃ can exert a complicated influence on plant phenotypic plasticity. In the present study, soil CaCO₃ additions all had remarkable effects on the RGR values of plant height, shoot-leaf biomass and root length of *A. ordosica* seedlings, and so did the soil available P concentrations when soil CaCO₃ contents were high. Higher soil CaCO₃ contents led to reduced growth in the plant height, root length, shoot-leaf biomass and root biomass of *A. ordosica* seedlings. In other words, soil CaCO₃ could affect the phenotypic plasticity of *A. ordosica* seedlings. This finding is an interesting phenomenon, as the molecule of CaCO₃ in the soil itself is neutral. How could it have influenced the growth rate of *A. ordosica* seedlings? One plausible explanation is that CaCO₃ made the soil "tighter", causing it hold more water, which could have hindered the ability of *A. ordosica* seedlings to absorb it, thus adversely affecting the growth of seedlings. Another mechanistic explanation is that the added CaCO₃ strongly reduced P availability in soil, which further limited the growth of the water-limited *A. ordosica* seedlings. Clearly, irrespective of how

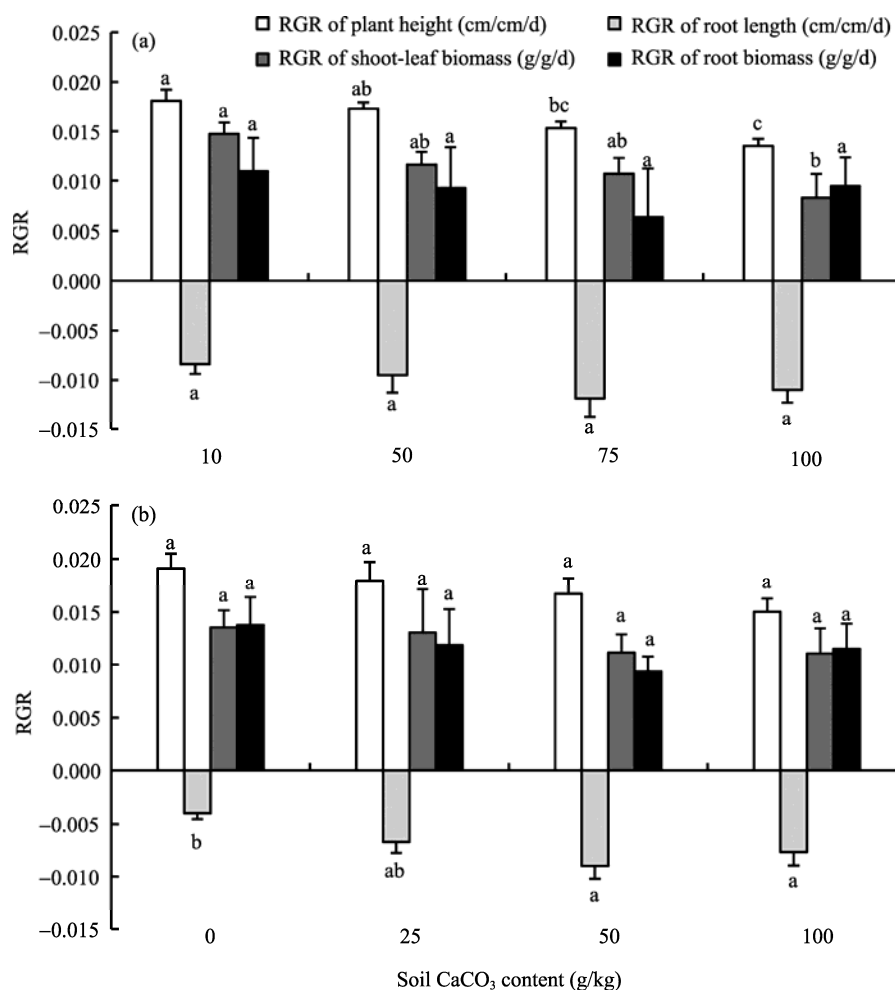


Fig. 2 Growth responses of *Artemisia ordosica* seedlings in the two-factor randomized block experiment (a) and orthogonal experiment (b) with high soil CaCO₃ content. Different lowercase letters indicate significant differences among soil CaCO₃ contents at $P < 0.05$ level. Bars mean standard errors.

it manifested, soil CaCO₃ additions reduced the growth potential of *A. ordosica* seedlings.

It is worth pointing out that the root length growth of *A. ordosica* seedlings gradually declined under higher soil CaCO₃ contents. So, the root length was constrained and not promoted with higher soil CaCO₃ contents, likely because during the early seedling growth of *A. ordosica*, the anterior extremity of their roots were decayed. When *A. ordosica* seedlings were transferred to the PVC pots (filled with sandy loam soil containing CaCO₃) from the seedling-raising pan (filled with a 1:1 mixture of turf:perlite), some decayed roots probably died. Moreover, with high CaCO₃ content in soil, more decayed roots died off. Thus, CaCO₃ additions prevented root length expansion in *A. ordosica* seedlings.

Kerley (2000) observed that *Lupinus albus* exhibited growth plasticity when it was exposed to a limed-soil profile. In our study, with increased soil CaCO₃ contents, the plant height, root length, shoot-leaf biomass and root biomass of *A. ordosica* seedlings progressively decreased. During the 40-d growth period, relative to the control, the plant height, root length, shoot-leaf biomass and root biomass of *A. ordosica* seedlings treated with 50 g/kg soil CaCO₃ decreased by 69.29%, 46.18%, 87.88% and 66.75%, respectively, with corresponding RGR reductions of 89.99%, 145.41%, 111.73% and 78.90%. Obviously, soil CaCO₃ can inhibit the growth plasticity of *A. ordosica* seedlings. In fact, it is well known that soil CaCO₃ is but one matrix of the soil formation and its influence on plant growth differs from other ecological factors such as light, temperature,

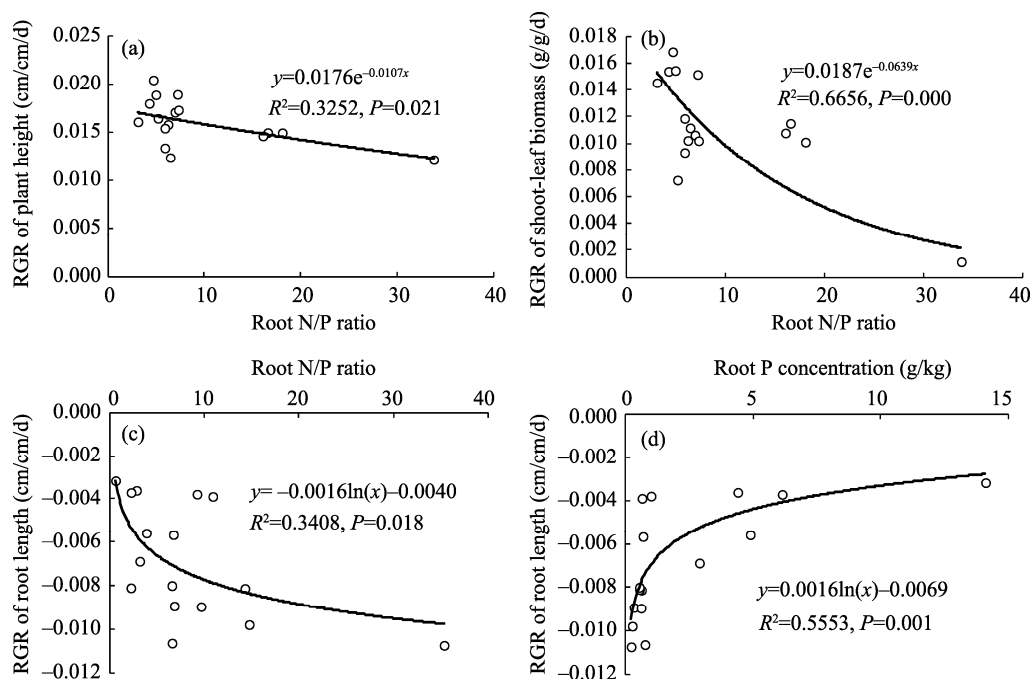


Fig. 3 Relationships (a) between RGR of plant height and root N/P ratio, and (b) between RGR of shoot-leaf biomass and root N/P ratio of *A. ordosica* seedlings in the high soil CaCO_3 content two-factor randomized block experiment; relationships (c) between RGR of root length and root N/P ratio and (d) between RGR of root length and root P concentration of *A. ordosica* seedlings in the high soil CaCO_3 content orthogonal experiment

water, heat, wind, soil nutrient and soil salinity (Fan et al., 2012; Zheng et al., 2012). Our results suggest that soil CaCO_3 is an abiotic stress factor for *A. ordosica* plants distributed in arid and semi-arid areas of Northwest China. As pointed out by Ghalambor et al. (2007), an adaptive phenotypic plasticity favors those plants establishing in new habitats, while a non-adaptive phenotypic plasticity corresponds with a stressful environment. In this respect, soil CaCO_3 appears to generate a non-adaptive phenotypic plasticity.

The inhibition by soil CaCO_3 on the growth plasticity of *A. ordosica* seedlings was essentially due to restrictions on their P absorption. We know that for calcareous soil in arid and semi-arid areas, approximately 70% of the total inorganic P consists of a Ca-P combination state (Ma et al., 2009). Among the pool of soil inorganic P, only $\text{Ca}_2\text{-P}$ was used here to simplify the more complicated form of 0.5 M NaHCO_3 (pH 7.5)-soluble P, which can significantly affect the level of soil available P (Ma et al., 2009). Accumulation of soil CaCO_3 maintains the soil pH at around 7.0–8.0, which can reduce P availability and thus restrict the plant P utilization rate (Reinbott and Blevins, 1999; Li et al., 2004; Wojewodzic et al., 2011). The main reason that P restriction leads to the inhibition of plant growth (Ehlers et al., 2010; Persson et al., 2011; Cai et al., 2012) is that it changes the plant C/N/P stoichiometry (Chen et al., 2010; Elser et al., 2010; Rivas-Ubacha et al., 2012). In arid and semi-arid areas, where P is of great importance to plant growth (Pajaei et al., 2018), a changed P concentration could alter the N/P ratio in the body of plant (He et al., 2016; Martinez-Oro et al., 2017). The growth rate hypothesis proposed by Elser et al. (2010) states that the specific growth rate of plant is negatively related to its N/P ratio (Matzek and Vitousek, 2009). In our study, with higher N/P ratios in *A. ordosica* seedlings, the RGR values of growth response variables (plant height, root-leaf biomass and root length) declined, which are consistent with the growth rate hypothesis.

The plant root is particularly sensitive to environmental change (Qiu et al., 2017). In the present study, the root length of *A. ordosica* seedlings showed a negative increase with higher soil CaCO_3 contents. Our follow-up analysis suggested that the root length growth of *A. ordosica* seedlings increased with greater P concentrations in their roots. This result implied that the way

that root N/P ratio influenced the RGR of root length occurred via soil CaCO_3 influence upon P absorption of *A. ordosica* seedlings. Thus, higher contents of soil CaCO_3 resulted in lower P concentrations in *A. ordosica* seedlings, and hence affected their phenotypic plasticity.

5 Conclusions

Soil CaCO_3 is clearly a stress factor that adversely affects the growth of *A. ordosica* seedlings. Irrespective of lower (<50 g/kg) or higher (>50 g/kg) CaCO_3 contents, CaCO_3 additions in soil can slow the growth of *A. ordosica* seedlings. Therefore, soil CaCO_3 could produce a non-adaptive phenotypic plasticity in *A. ordosica* seedlings. Under higher soil CaCO_3 contents, with an increase in root N/P ratio, the RGR values of plant height, shoot-leaf biomass and root length all decreased significantly, but with an increase in root P concentration, the RGR of root length increased significantly. Hence, a changed root P concentration is the main driver responsible for producing phenotypic plasticity in *A. ordosica* seedlings.

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